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ANTS ASSOCIATED WITH A COLEOPTEROUS LEAF-BUD GALL ON *XYLOPIA AROMATICA* (ANNONACEAE)

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Abstract.—We describe the ant fauna (11 species divided into four genera) associated with a coleopterous leaf-bud gall on *Xylopia aromatica* (Annonaceae) in Minas Gerais, Brazil. Ant occupied galls are significantly larger than are unoccupied galls, and the variance of gall diameters for occupied galls is significantly smaller than is the variance for all galls. There is a significant positive relationship between ant colony size and gall diameter. The six most common species of ants may partition galls according to gall size, as there are significant differences in the diameters of occupied galls among species. At the community level, patterns of co-occurrence of ants are indistinguishable from those expected under a random assortment model. Individual ant species do exhibit non-random patterns of co-occurrence.

Key Words: Annonaceae, ants, Brazil, coleopterous gall, community ecology, habitat selection, insect galls, Minas Gerais, resource partitioning, *Xylopia aromatica*

Plant galls represent an important resource for many species other than the gall formers. Owing to their localized concentration of nutritive tissues and their marked succulence, galls provide favourable breeding sites for a variety of species (Brandhorst 1962, Mani 1964, Shorthouse 1973, Yukawa 1983). Galls protect their inhabitants from inclement weather (Felt 1940, Uhler 1951, Sandlant 1979; but see Baust et al. 1979) and natural enemies (Askew 1961, 1980, but see Price et al. 1986, 1987). Use of galls ranges from species that open galls simply to prey upon gall formers and inquilines to those that depend exclusively on gall tissues for food and shelter.

Beauvisage (1883, cited in Mani 1964) applied the term "locatari" to species, other than the gall formers, associated with insect galls. Mani (1964) divides the locatari into 33 categories according to their ecological niches. The locatari often represent a vast fauna with the most numerous categories consisting of parasites and predators. For example, Stegagno (1904) reported 177 species associated with cynipid galls on *Quercus* in Italy; of these, 138 are parasites and predators.

Species that inhabit galls after emergence of gall formers and inquilines are the "successori" (Mani 1964, Yukawa 1983). Most of these are plant-nesting ants and myrmecophilous insects, such as aphids and coccids. Others include mites, spiders, thrips, collembola, bees, and wasps (reviewed by Mani 1964). The most common ant genera associated with old galls are: *Camponotus, Cataulacus, Crematogaster,*

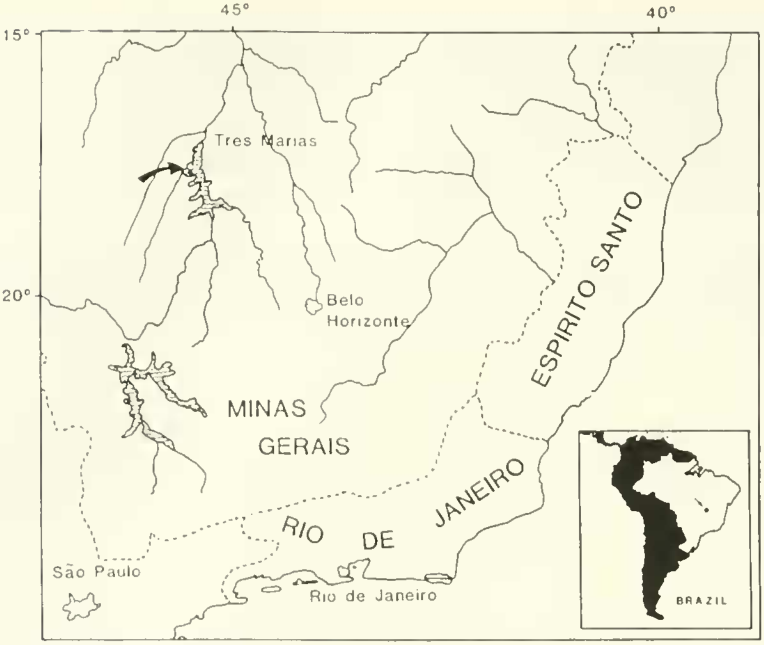

Fig. 1. Location of the Ecological Station of Parapitinga in Três Marias, Minas Gerais, Brasil.

Colobopsis, *Lasius*, *Leptothorax*, and *Olopsis* (Walsh 1864, Patton 1879, Wheeler 1910, Ping 1920, Sturtevant 1925, Mani 1964, Torossian 1971a, b). Despite their importance and dominance within the successori, little is known about the ecologies of these ants other than compendiums of ant species associated with particular species of gall formers (e.g. Brandhorst 1962, Espadaler and Nieves 1983).

Here, we describe the ant fauna associated with a coleopterous leaf-bud gall on *Xylopia aromatica* (Annonaceae). We describe patterns in distribution and abundance of the ant fauna and document elements of habitat selection and resource partitioning.

Material and Methods

One of us (G.W.F.) collected galls from the Ecological Station of Parapitinga, Três Marias, Minas Gerais, Brazil during one sample period in mid-May, 1984. The station is a continental island located in a man-made lake (Três Marias Lake) between latitude 18°–19° south and longitude 45°–46° west (Fig. 1).

The host tree, *Xylopia aromatica*, occurred in a gallery forest along the northwest border of the island. Only three individuals of approximately six meters tall bearing galls were observed in the area surveyed. The galls are induced by an unidentified species of curculionid (Coleoptera). Gall formers held as vouchers were kept in the author's collection. The galls are spherical and glabrous and occur on leaf-buds (Fig. 2). They are green when occupied by the gall former, but turn brown after its emergence. All galls which were on trees (n = 114) were collected and subsequently measured and dissected in the laboratory. Galls that fall on the forest floor are also utilized by ants; however they are not included here because of insufficient sample size.

In this paper, we use the word "colony" as any group of ants, composed of workers and larvae (eggs, queen, and pupae if pres-

Fig. 2. Coleopterous leaf-bud galls found on *Xylopia aromatica*. Gall diameter ranged from 5.0 to 21.5 mm.

ent), occupying a single gall. In addition, we defined those galls in which we found only workers as "groups of workers."

STATISTICAL ANALYSES

We compared the mean diameter of galls that were occupied by ants with the mean diameter of unoccupied galls using one-way analysis of variance. We also compared the variance of occupied galls with the variance of all galls (including occupied galls) with a Chi-square test (Sokal and Rohlf 1969, page 175). We assumed that our collection consisted of the entire population of galls on the island and that the set of occupied galls was a sample from that population.

Table 1. Ant species associated with coleopterous leaf-bud galls on *Xylopia aromatica* (Annonaceae).

Ant Species	Number of Colonies	($\bar{x}$) Individuals Adult	Larvae/Pupae	Gall Diameter ($\bar{x}$) mm
Azteca bicolor	1	1.0	—	14.5
Azteca sp.	17	28.1	8.9	16.4
Leptothorax wilda	13	5.4	4.6	14.7
Leptothorax sp.	1	45.0	37.0	17.0
Pseudomyrmex flavidus	4	0.8	5.5	16.4
Pseudomyrmex sp. A	1	1.0	—	12.5
Pseudomyrmex sp. B	1	1.0	—	15.0
Zacryptocerus pallens	7	2.0	—	12.9
Zacryptocerus pusillus	8	51.3	12.5	15.9
Zacryptocerus sp. A	11	5.7	2.2	14.9
Zacryptocerus sp. B	1	4.0	4.0	10.0

We compared the mean diameters of occupied galls among the six most common species of ants by one-way analysis of variance.

We estimated the relationship between the logarithm of colony size (number of individuals, of all castes, in a gall) and gall diameter through linear regression.

Finally, we examined patterns of occurrence within galls. We compared the number of galls that contained 0, 1, 2, and 3 species of ants with those expected under a Poisson distribution. We estimated λ, the Poisson parameter, from the sample. We compared the observed distribution to the expected distribution with a Chi-square goodness-of-fit test.

RESULTS

We collected 114 galls of which 52 (45.6%) were occupied by ants. Eleven species of ants were represented in the sample; the most common were *Azteca* sp. which occupied 17 galls, *Leptothorax wilda* which occupied 13 galls, and *Zacryptocerus* sp. "A" which occupied 11 galls (Table 1). Five species were represented by a single individual. "Colony sizes" ranged from three individuals to a colony of *Zacryptocerus pusillus* which contained 129 adults and larvae.

The internal structure of the galls was highly modified in some cases, unmodified in others (Fig. 3). Modification is defined as any internal architectural departure, such as tunnel and gall wall holes, from the usual spheroid larval chamber. In particular, galls inhabited by *Azteca* sp. and *Zacryptocerus pusillus* exhibited extensive modifications when compared to unmodified galls. Galls inhabited by *Pseudomyrmex flavidus* were unmodified. Modified galls typically contained larger colonies than did unmodified galls.

Ants typically occupied large galls (Fig. 4). The mean diameter of occupied galls, 15.6 mm, was significantly larger than the mean diameter of unoccupied galls, 13.6 mm ($F_{1,112} = 12.8$, $P < 0.001$). The variance of diameters of occupied galls was significantly smaller than would be expected if ants were selecting galls at random ($\chi^2_{113} = 72.1$, $P < 0.005$).

There was a significantly positive linear relationship between the logarithm of colony size (number of individuals) and gall diameter (Fig. 5).

The six more common species of ants further partitioned the subset of occupied galls according to gall size; mean gall diameters of occupied galls were significantly different among species ($F_{5,54} = 2.74$, $P < 0.05$). *Azteca* sp. typically occupied the largest galls ($\bar{x} = 16.4$ mm), *Zacryptocerus pallens* the smallest ($\bar{x} = 12.9$ mm).

We collected 65 colonies distributed

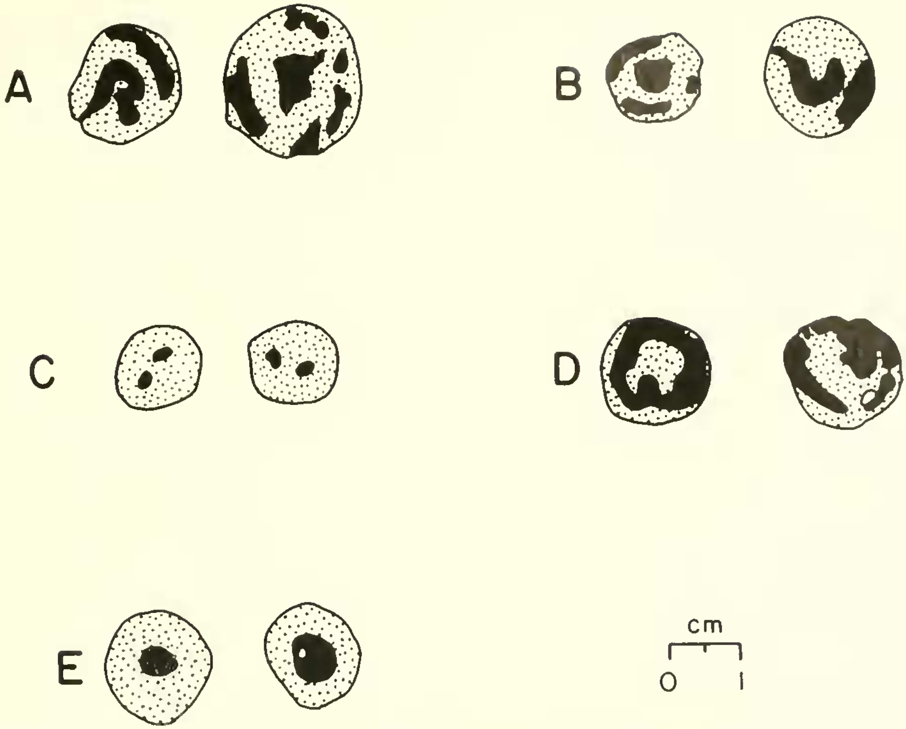

Fig. 3. Cross-sections of galls showing internal modifications by ants. Gall (A) contained *Azteca* sp., (B) *Leptothorax* sp., (C) *Zacryptocerus pallens*, (D) *Zacryptocerus pusillus*, and (E) *Pseudomyrmex flavidus*.

among 114 galls. We estimated λ, the Poisson parameter, as 65/114 = 0.57. The observed distribution of colonies among galls closely resembled the expected under a Poisson distribution (Table 2). The goodness-of-fit test indicated no significant difference between the observed and expected distributions ($\chi^2_3 = 2.51$, $P > 0.10$).

Individual species did exhibit frequencies of co-occurrence that appeared different from those expected by chance alone (Table 3). For example, *Zacryptocerus pusillus*

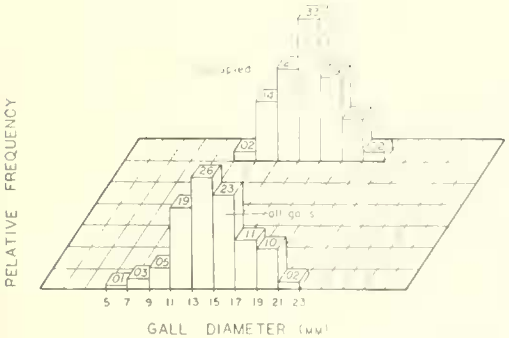

Fig. 4. Relative frequency histograms of gall diameter for the entire set of galls (foreground) and for the subset of galls that were occupied by ants (background).

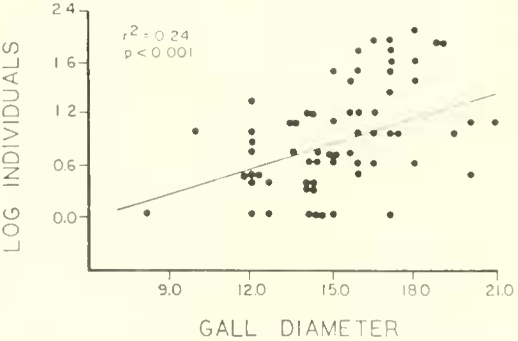

Fig. 5. Relationship between the logarithm of colony size (number of individuals) and gall diameter. The relationship is $\hat{Y} = -0.929 + 0.122\hat{X}$ ($F_{1,63} = 20.1$, $P < 0.001$; $R^2 = 0.24$).

Table 2. Distribution of colonies among galls. Expected values are based on a Poisson distribution with $\lambda = 0.57$.

Colonies/Gall	Observed	Expected
0	62	64.5
1	42	36.8
2	7	10.5
3	3	2.0

never jointly occupied a gall, while approximately 4 such co-occurrences would be expected at random. *Azteca* sp. and *Leptothorax wilda* were roughly half as likely to co-inhabit a gall as chance alone would predict. On the other hand, *Zacryptocerus pallens* exhibited a slight tendency to share galls.

Table 3. Patterns of co-occurrences among ant species.

Species	Joint Occurrences	
	Observed	Expected
Azteca bicolor	1	0.58
Azteca sp.	4	7.15
Leptothorax wilda	3	5.93
Leptothorax sp.	0	0.58
Pseudomyrmex flavidus	3	2.13
Pseudomyrmex sp. A	1	0.58
Pseudomyrmex sp. B	0	0.58
Zacryptocerus pallens	5	3.54
Zacryptocerus pusillus	0	3.99
Zacryptocerus sp. A	5	5.19
Zacryptocerus sp. B	0	0.58

DISCUSSION

Galls represent an important resource for this ant community, and ants exploit this resource in a non-random fashion. Ants select significantly larger galls, over a narrower range of sizes, than chance alone would predict. Both the difference in means and the difference in variance indicate habitat selection. There may be strong selective pressures for this habitat selection as indicated by the significant positive relationship between colony size and gall size. Selection of larger galls by ants may be due to several reasons, among them increase in queen fitness. However, more work is called for to observe the selection and the use of larger versus smaller galls.

It is not clear whether galls are a limiting resource to these ants. On the other hand, the most common species of ants exhibited resource partitioning. This is a necessary condition for stable coexistence of multispecies assemblages exploiting similar, limiting resources predicted by Lotka-Volterra based analyses of community dynamics (May 1973, Schoener 1974). Of course, neither observation by itself is conclusive. Unoccupied galls may be the result of interference competition or priority effects (sensu Torres 1984). Significant differences among species in the diameters of occupied galls may not be the result of competitively induced resource partitioning, but rather, species' idiosyncratic responses to their environment (James et al. 1984). Correlative data provide notoriously weak inferences regarding mechanisms (Brady 1979); experiments are required to establish causation.

Patterns of species co-occurrence at the community level are indistinguishable from those predicted from a random assortment model. However at the constituent level, individual species deviate from expectation. In particular, *Zacryptocerus pusillus* never shares a gall, although approximately four joint occurrences are predicted. Fowler et al. (1985) provide evidence that *Z. pusillus* is interspecifically territorial. Whether deviations from chance for the other species are biologically significant is unclear. Unfortunately, little is known about the ecologies of these ants.

Gall-inhabiting ants may provide an ideal system to examine the determinants of community organization in arboreal ants. Galls are a discrete resource, amenable to experimental manipulation in time and space.

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